Simulating the impacts of southern pine beetle and fire on the dynamics of xerophytic pine landscapes in the southern Appalachians

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Abstract

Question: Can fire be used to maintain Yellow pine (*Pinus* subgenus *Diploxylon*) stands disturbed by periodic outbreaks of southern pine beetle?
Location: Southern Appalachian Mountains, USA.
Methods: We used LANDIS to model vegetation disturbance and succession on four grids representative of xeric landscapes in the southern Appalachians. Forest dynamics of each landscape were simulated under three disturbance scenarios: southern pine beetle, fire, and southern pine beetle and fire, as well as a no disturbance scenario. We compared trends in the abundance of pine and hardwood functional types as well as individual species.
Results: Yellow pine abundance and open woodland conditions were best maintained by a combination of fire and southern pine beetle disturbance on both low elevation sites as well as mid-elevation ridges & peaks. On mid-elevation SE-W facing slopes, pine woodlands were best maintained by fire alone.
Conclusions: Our simulations suggest that fire can help maintain open pine woodlands in stands affected by southern pine beetle outbreaks.

Keywords: *Dendroctonus frontalis*; Forest disturbance; Forest restoration; LANDIS; Landscape modeling; *Pinus*; Vegetation dynamics.

Abbreviations: BDA = Biological disturbance agent; SPB = Southern pine beetle; SRD = Site resource dominance; SRDm = Modified site resource dominance; SV = Site vulnerability.

Introduction

Disturbance events exert a strong influence on forest structure, composition, and diversity by killing trees and altering the availability of plant resources (Connell 1978; White 1979; Huston 1994). Many ecosystems are affected by multiple disturbances that create varying impacts on vegetation (Frelich 2002; Kulakowski & Veblen 2002; Platt et al. 2002; Howe & Baker 2003; Lafon & Kutac 2003), but the role these disturbance interactions play on landscapes is not well understood. The removal or alteration of one or more of these disturbance processes can serve as a successional catalyst, driving the change from one ecosystem or community type to another (Holling 1992).

Xeric slopes and ridges in the southern Appalachians serve as an example of the importance of multiple interacting disturbance regimes on ecosystem function as they have historically been maintained as open pine woodlands through a process involving multiple interacting disturbances (Barden & Woods 1976; Kuykendall 1978; White 1987; Smith 1991; Williams 1998). These open pine woodland ecosystems are now at risk from successional pressure by hardwoods due to a change in the southern pine beetle, *Dendroctonus frontalis* (*Coleoptera*: *Curculionidae*), and fire disturbance regime that once characterized this area. In particular, fire suppression efforts have initiated a shift toward dense forest stands with an understory of young hardwood trees that will most likely replace the pines over time (Harrod et al. 1998, 2000; Lafon & Kutac 2003). As a result, these communities are undergoing both changes in species composition and changes in landscape structure.

Assessing the consequences of multiple interacting disturbances on successional trajectories is challenging due to the large spatial and temporal scales involved.

While empirical field observation and experimentation is not feasible, computer simulation models offer a means for exploring the long-term implications of different disturbance scenarios. In this paper, we use LANDIS 4.0 (hereafter LANDIS), a computer model for simulating disturbance and succession on forest landscapes, to investigate the role of two types of disturbance – fire and SPB outbreaks – in xerophytic Yellow pine (*Pinus* subgenus *Diploxylon*) forests of the southern Appalachian Mountains, USA. Understanding the relationship between fire, insect disturbance, and mesoscale forest landscape dynamics (scale of processes: several to tens of km and years to decades; Holling 1992) will not only provide insight as to the processes involved in shaping southern Appalachian ecosystems, but will also add to the general conceptual issues surrounding multiple disturbance interactions. Moreover, because land managers are increasingly using prescribed burning as a restoration tool in the southern Appalachian Mountains (Pyne 1982; Anon. 1996; Williams 1998; Haines & Busby 2001; Palik et al. 2002; van Lear & Brose 2002) without knowing its implications on long-term forest dynamics, we demonstrate the utility of our modeling approach to forest restoration efforts.

Background

The southern Appalachians extend from northern Georgia to southern Virginia and can be described as mountainous with a humid, continental climate (Bailey 1978). Because of the topographic variation, temperature and precipitation exhibit pronounced microscale spatial patterns. Community types range from mesophytic *Tsuga* (*canadensis, carolinia*)-hardwood forests on valley bottoms, to xeric Yellow pine woodlands on ridge tops; and from low-elevation temperate deciduous forests to high-elevation *Picea-Abies* (spruce-fir) stands (Whittaker 1956; Stephenson et al. 1993).

Fire was historically important in shaping the vegetation communities in the southern Appalachians (Harmon 1982; Randles et al. 2002; Waldrop et al. 2002). Detailed records of fire history have been constructed for the past 150-400 years using dendro-ecological techniques (Harmon 1982; Sutherland et al. 1995; Shumway et al. 2001; Armbrister 2002; Shuler & McClain 2003). These studies suggest that surface fires burned at intervals of about 5-15 years in pine and oak woodlands of the southern and central Appalachian Mountains. More intense stand-replacing fires are also known to have occurred. These fire history analyses also reveal a marked decline in fire frequency during the mid-1900s which is associated with efforts to exclude fire from the forests.

Indigenous to the southern USA, southern pine beetle (SPB) can infest *Pinus rigida*, *P. virginiana*, *P. pungens*, and occasionally *P. strobus* in the southern Appalachian Mountains (Payne 1980; Coulson et al. 1999; Coulson & Wunneburger 2000). Multiple-tree infestations often develop in stands occurring on sites with poor nutrient and/or moisture content that contain mature host species with high basal area and stagnant radial growth. Such stands are considered to be at high hazard for infestation (Mason et al. 1985). Outbreaks are centered initially in high-hazard stands, but when populations of the insect become large, less preferred hosts occurring on low-hazard sites are also infested.

Outbreaks of SPB occur periodically. In the Piedmont and Coastal Plain, outbreaks generally occur on a 7-10 year cycle (Price et al. 1998). In the southern Appalachians, outbreaks are less frequent and occur on 10-25 year cycles. Causes for SPB outbreaks are poorly understood but when favorable environmental conditions coincide with optimal resource availability, populations increase in size and outbreaks often follow (Rykiel et al. 1988).

The xeric slopes and ridges of the southern Appalachian Mountains are dominated by Yellow pines (*Pinus*) and oaks (*Quercus*). It has been suggested that SPB outbreaks are a key factor in driving the succession of these yellow pine woodlands (Harmon 1980; Harrod et al. 1998, 2000; Williams 1998). When disturbances, such as ice storms and SPB outbreaks, impact xeric pine-oak forests, the successional trend may be towards oak domination (Williams 1998). However, when fire is also present, the successional trend will be towards pine domination, maintained in a drought-beetle-fire cycle (Barden & Woods 1976; Kuykendall 1978; White 1987; Smith 1991; Williams 1998). For instance, Lafon & Kutac (2003) discovered that pine populations were heavily reduced and pine regeneration was absent on xeric sites disturbed by ice storms and SPB; however, abundant regeneration occurred on neighboring sites disturbed by ice, SPB, and fire. While SPB may aid in regenerating pines by adding to fuel loads under an active fire regime, they may reduce pine populations in the absence of fire (Kuykendall 1978; Williams 1998). A relationship between fire and SPB has been suggested (Showalter et al. 1981), but is not yet fully understood. Over long time periods, fire reduces tree density and creates more open woodland conditions (Delcourt & Delcourt 1998; Harrod et al. 2000). Such low-density spacing would be unfavorable to severe SPB outbreaks.

Methods

Model description

LANDIS (LANdscape DIsturbance and Succession) is a raster-based spatially explicit computer model designed to simulate forest succession and disturbance across broad spatial and temporal scales (Mladenoff et al. 1996; He et al. 1996, 1999a, b; He & Mladenoff 1999a, b; Mladenoff & He 1999). Originally developed to simulate succession as well as harvesting, windthrow, and fire disturbance on the glaciated plains of the upper Midwest (Mladenoff 2004), LANDIS has been successfully adapted for use in a variety of locations (Shifley et al. 1998; Franklin et al. 2001; He et al. 2002; Pennanen & Kuuluvainen 2002; Pennanen et al. 2004; Schumacher et al. 2004; Wimberley 2004). Recently, we have demonstrated the utility of LANDIS in modeling the effects of fire on pine and oak forests in the southern Appalachians (Lafon et al. In press).

Landscapes in LANDIS are subdivided into land types which contain environmentally specific parameters regarding species establishment as well as disturbance behavior. These land types are then further subdivided into individual sites or cells. Tree species are simulated as the presence or absence of ten-year age cohorts on each cell. At the site (cell) level, LANDIS manages user-defined species life history traits (longevity, minimum age at reproduction, shade tolerance, fire tolerance, min/max seed dispersal distances, and resprout probability) at ten-year time steps. Succession is based on the species specific characteristics of dispersal, shade tolerance, and habitat suitability. Disturbance can be modeled in terms of fire, wind, harvesting, and biological agents (insects, disease; Sturtevant et al. 2004a).

Fire is modeled in LANDIS as hierarchical stochastic processes based on fire ignition, fire initiation, and fire spread (Yang et al. 2004). The number of ignitions on a given land type is specified as the average number per decade. Fire initiation occurs if the probability of ignition, which is determined by the time since the last fire, is sufficient to generate a fire. Once fire initiation occurs, fire is spread in the cardinal directions until it reaches its maximum possible user-defined size or until it reaches a break (Yang et al. 2004). Fire severity is an integer between 1 (least severe) and 5 (most severe) and is determined by the time passed since the last fire event on each cell. Probability of mortality from fire is a function of tree age and species whereby low-intensity fires kill young/fire-intolerant species, while fires of higher intensity kill larger trees and more fire-tolerant species (He & Mladenoff 1999b).

Biological disturbances in LANDIS are modeled using the Biological Disturbance Agent (BDA) module. Biological disturbances are probabilistic at the site (cell) level. Each site is assigned a Site Vulnerability (SV) probability value that is checked against a uniform random number to ultimately determine if that site has been affected by a biological agent. Site vulnerability can either be directly equated with the Site Resource Dominance (SRD) value which ranges from 0-1 and is based on species and species age, or it can also be modified by three variables to determine the impact on a given site. The first of these variables is the Modified Site Resource Dominance (SRDm) which determines the presence of susceptible hosts based on stress from other disturbance or environmental factors. The second factor, Neighborhood Resource Dominance (NRD), determines the effect of hosts/non-hosts in neighboring cells. The third factor is the periodicity of outbreaks which can either be chronic, cyclic, or random.

The study of forest pattern, structure, and succession is scale dependant. LANDIS is an effective tool for generalizing forest succession on mesoscale landscapes. At these scales, disturbance processes such as fire and insect outbreaks dominate the formation of vegetation pattern (Holling 1992). It is important to note, however, that these generalizations, while important, neither apply to microscale processes that may be occurring at sub-annual and sub-meter levels nor to macroscale processes that may influences forest dynamics at 100s of km or centuries to millennia (Holling 1992).

Model simulations

Great Smoky Mountains National Park (GSMNP) serves as a model for the idealized landscapes we simulate. GSMNP is a 2110 km^2 World Heritage Site and International Biosphere Reserve straddling the border between western North Carolina and eastern Tennessee. GSMNP serves as an ideal model for this study as most major ecosystems of the southern Appalachians are represented, and the general topographic distribution of communities and tree species have previously been described (Whittaker 1956).

We used LANDIS to simulate forest dynamics over a 1000-year period on low and mid elevation xeric landscapes. To capture the predominant elevation and moisture gradients that influence vegetation distribution in the southern Appalachians, we used hypothetical landscapes. Each landscape comprised a single land type represented by a 100 × 100 cell grid with a cell size of 10 m × 10 m. We distinguished four land types that correspond to two elevation zones (low: 400-915 m and middle: 916-1370 m) and two topographic moisture classes (SE-W facing slopes; ridges and peaks) in the Great Smoky Mountains (Whittaker 1956). Hypothetical landscapes are commonly used in simulation modeling studies to facilitate

model interpretation on a controlled environment (e.g. Mladenoff & He 1999; Pennanen et al. 2004; Syphard & Franklin 2004). For this study we used a simple grid environment to glean information on within-land type successional dynamics without the influence of spatial complexities. By first understanding succession and process behavior on simple landscapes, we will later be able to better interpret subsequent modeling investigations with more complex spatial arrangements.

We included 15 tree species in our simulations (Table 1). Life history parameters were based on Burns & Honkala (1990), which has served as the basis for a number of previous forest modeling studies (e.g., Lafon 2004; Sturtevant et al. 2004b; Wimberly 2004). These life history traits were further altered to reflect species responses specific to the southern Appalachian Mountains (David Loftis & Henry McNab, Bent Creek Experimental Forest, Asheville, NC, unpubl. data). Because we were not investigating dispersal effects for this study, identical dispersal capabilities (0.95 within 20 m and 0.05 between 20 and 40 m) were assigned to all species to minimize the influence of dispersal effects on model projections. Establishment coefficients were based on the abundance of tree species along the elevation and moisture gradients in the Great Smoky Mountains (Whittaker 1956). These initial abundance values were further modified by drought and shade tolerance parameters to obtain species-specific establishment coefficients for each land type (Lafon et al. In press).

The initial abundance of species on each land type was based on the relative abundance of the species following Whittaker (1956). Each 100-m^2 cell was then populated randomly with a single species based on its relative abundance in each of the land types (Fig. 1).

We simulated three disturbance scenarios: (1) SPB,

(2) historic fire regime, and (3) SPB with historic fire regime. A non-disturbance scenario was added for comparison. For the historic fire regime, target fire return intervals for each land type were derived from dendro-ecological reconstructions of past fire return intervals in Yellow pine forests of the southern Appalachian Mountains (Harmon 1982; Sutherland et al. 1995; Armbrister 2002). The return interval for each land type was calibrated by adjusting fire parameters until the mean return interval for ten 1000-year simulations was within 10% of the target interval of ten years on xeric sites (cf. Wimberly 2004; Lafon et al. In press). Because the available fire history information is insufficient to distinguish among the fire regimes of the four simulated land types, fire severity curves were identical for all four landscapes with class-2 fires occurring after 10 years, class-3 fires after 30 years, class-4 fires after 60 years, and class-5 fires after 120 years without burning.

The BDA module was parameterized to mimic SPB outbreaks in the southern Appalachians. Each of the pine species in the model (*P. pungens*, *P. rigida*, *P. virginiana*, and *P. strobus*) was assessed for its vulnerability to SPB attack. Vulnerability in LANDIS is defined by tree age. Vulnerability of southern Appalachian yellow pine species to attack by SPB is correlated to tree diameter (Coulson et al. 1974; Table 2). Growth rates were generalized for the southern Appalachians to arrive at vulnerability ages (Brian Kloeppel, Coweeta LTER Co-Lead Principal Investigator, pers. comm. November 11, 2004; Table 2). These data were then rounded to the appropriate ten-year age cohort class for LANDIS input.

For these simulations, we modified vulnerability by fire. Because of subsequent density reduction, the dis-

Table 1. Species life-history parameters for 15 tree species (adapted from Burns & Honkala 1990). mxAge = expected longevity; mtAge = Age at reproductive maturity; shTl = shade tolerance (1-5, 1 denotes least shade tolerance); frTl = fire tolerance (1-5, 1 denotes least tolerance to fire); prRes = probability of resprouting; esPb = establishment probability (1 = low elevation SE-W facing slopes, 2 = low elevation ridges and peaks, 3 = mid elevation SE-W facing slopes, 4 = mid elevation ridges and peaks).

	mxAge	mtAge	shTl	frTl	prRes	esPb1	esPb2	esPb3	esPb4
Acer rubrum	150	25	4	1	0.9	0.08	0.04	0.152	0.076
Carya glabra	300	40	2	2	0.5	0.063	N/A	0.211	N/A
Nyssa sylvatica	200	25	4	2	0.3	0.115	0.057	0.229	N/A
Oxydendrum arboreum	100	50	3	2	0.9	0.115	0.057	0.229	0.115
Pinus pungens	250	20	1	5	0.3	N/A	0.002	0.083	0.083
Pinus rigida	200	25	1	5	0.3	0.083	0.075	0.065	0.065
Pinus strobus	400	25	3	2	0	0.151	0.113	N/A	N/A
Pinus virginiana	100	20	1	4	0.1	0.083	0.075	N/A	N/A
Quercus alba	450	30	3	3	0.5	0.016	N/A	0.08	N/A
Quercus rubra	300	25	2	3	0.4	0.018	N/A	0.211	0.106
Quercus coccinea	130	25	1	3	0.4	0.083	0.075	0.041	0.041
Quercus prinus	350	25	3	3	0.9	0.115	0.053	0.115	0.057
Quercus velutina	150	25	2	3	0.7	0.106	N/A	0.106	N/A
Robinia pseudoacacia	100	15	1	1	0.9	0.188	0.094	0.375	0.188
Tsuga canadensis	450	50	5	1	0	0.008	N/A	N/A	N/A
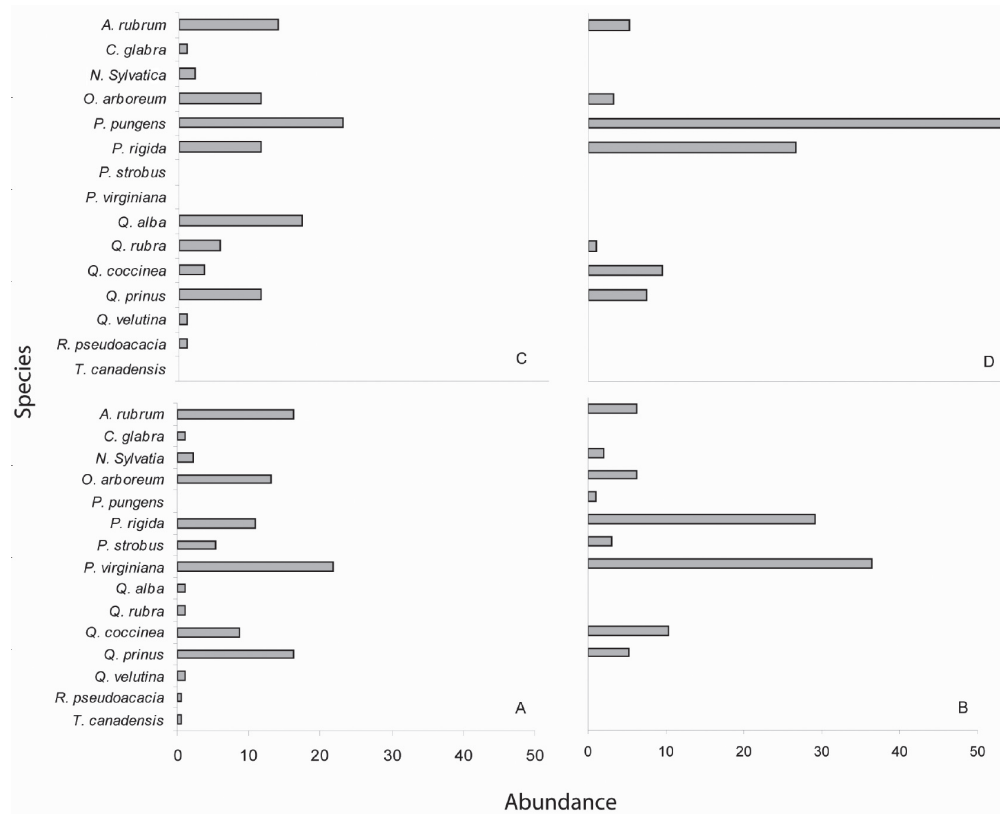
Fig. 1. Initial abundance (% of grid cells occupied) of 15 tree species in each landscape. (A) low-elevation SE-W facing slopes, (B) low-elevation ridges and peaks, (C) mid-elevation SE-W facing slopes, (D) mid-elevation ridges and peaks. See Table 1 for full species names.

turbance modifier, which can range from –1 to +1, was set equal to –1 for 20 years following fire. The radius of influence for the Neighborhood Resource Dominance was set to 30 m, which is consistent with the attractiveness area of pines under bark beetle attack (Turchin 1998). The weight of the Neighborhood Resource Dominance was set to be equal to that of the Site Resource Dominance (Neighborhood Weight = 1). Timing of outbreaks was determined by a uniformly-distributed random number with a minimum interval of 10 years (smallest possible in LANDIS) and a maximum interval of 30 years, which

is consistent with historical SPB trends in the southern Appalachians. Outbreak severity, which is an integer between 0 (no activity) and 3 (severe outbreak), was set at a minimum of 1 and maximum of 3 for each 10-year time step as SPB activity is chronic and there is a high potential for SPB outbreaks to occur each decade.

Because LANDIS is a stochastic model, we generated ten sets of model runs for each disturbance scenario on each land type to account for potential variability. Each of the sets was created by varying the LANDIS seed variable by increments of 1000 for replication.

Table 2. Age and Diameter at Breast Height (DBH) of southern pine beetle (SPB) host vulnerability groups.

|	Minor host DBH	Minor host Age	Secondary host DBH	Secondary host Age	Primary host DBH	Primary host Age
Pinus pungens	~10.16 cm	20	~10.16 – 15.24 cm	35	> ~15.24 cm	50
Pinus rigida	~10.16 cm	15	~10.16 cm	15	> ~10.16 cm	20
Pinus virginiana	~10.16 cm	20	~10.16 – 15.24 cm	25	> ~15.24 cm	32.5
Pinus strobus	~10.16 cm	15	~10.16 – 20.32 cm	25	N/A	N/A

Results

Each of the four disturbance scenarios had distinct impacts on the abundance of pines in each of the four land types (Fig. 2). While there is some variation in results between the four land types, in general, SPB alone leads to the removal of pines and dominance of hardwoods, fire alone leads to the removal of hardwoods and dominance of pines, and the combination of SPB and fire tends to stabilize both pine and hardwood populations at levels near the initial conditions. In the no-disturbance scenario, hardwoods become dominant because of a combination of resprouting and shade tolerance (Fig. 2).

In addition to the dynamics of functional types, trends for individual pine species were also analysed (Fig. 3). The most distinctive difference was between the behavior of *Pinus strobus* and the three Yellow pine species. However, individual variations were present for all species and land types. In the low-elevation landscapes, *P. strobus* substantially increased in abundance in the absence of fire and in the presence of SPB but was removed from the landscape in the presence of fire and SPB/fire (Fig. 3C, G). *P. rigida* increased in abundance with presence of fire and maintained abundance with SPB/fire, but was removed from the landscape with SPB alone and with no disturbance (Fig. 3B, F). *P. virginiana*, which began as

the most dominant species, maintained abundance with fire and SPB/fire and was removed from the landscape with SPB disturbance only as well as with no disturbance (Fig. 3D, H).

On mid-elevation SE-W-facing slopes, both *P. rigida* and *Pinus pungens* (Fig. 3I, J) increased in abundance in the fire scenario. In the SPB/fire scenario, *P. rigida* declined, while *P. pungens* remained stable. *P. rigida* and *P. pungens* populations were reduced to zero in the SPB scenario and to near zero in the no disturbance scenario. On mid-elevation ridges and peaks, both *P. rigida* and *P. pungens* (Fig. 3M, N) increased in abundance with the presence of fire and were nearly removed with just SPB and no fire. In the SPB/fire scenario, *P. rigida* dropped in abundance while *P. pungens* maintained its abundance.

Based on the proportion of empty cells, the mixed SPB/fire scenario created and maintained open woodland conditions on ridges & peaks as well as on low elevation SE-W facing slopes (Figs. 4 and 5). Fire alone also created such conditions, although to a somewhat lesser extent. The SPB-only disturbance scenario resulted in a spatial arrangement suggestive of denser closed-canopy forests.
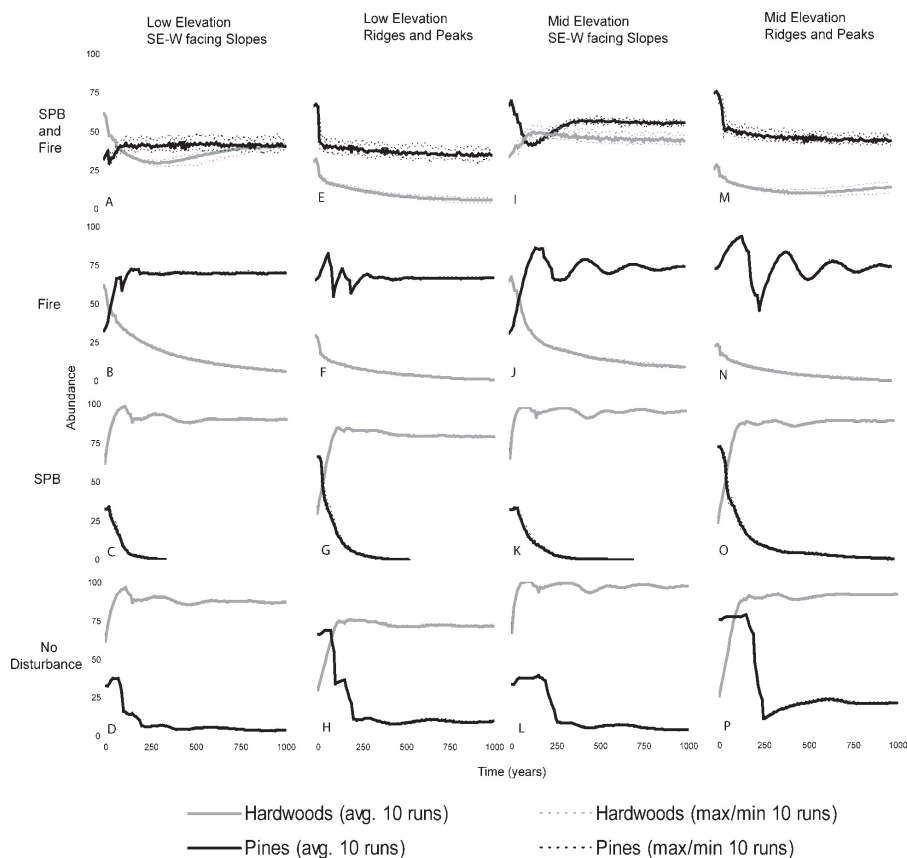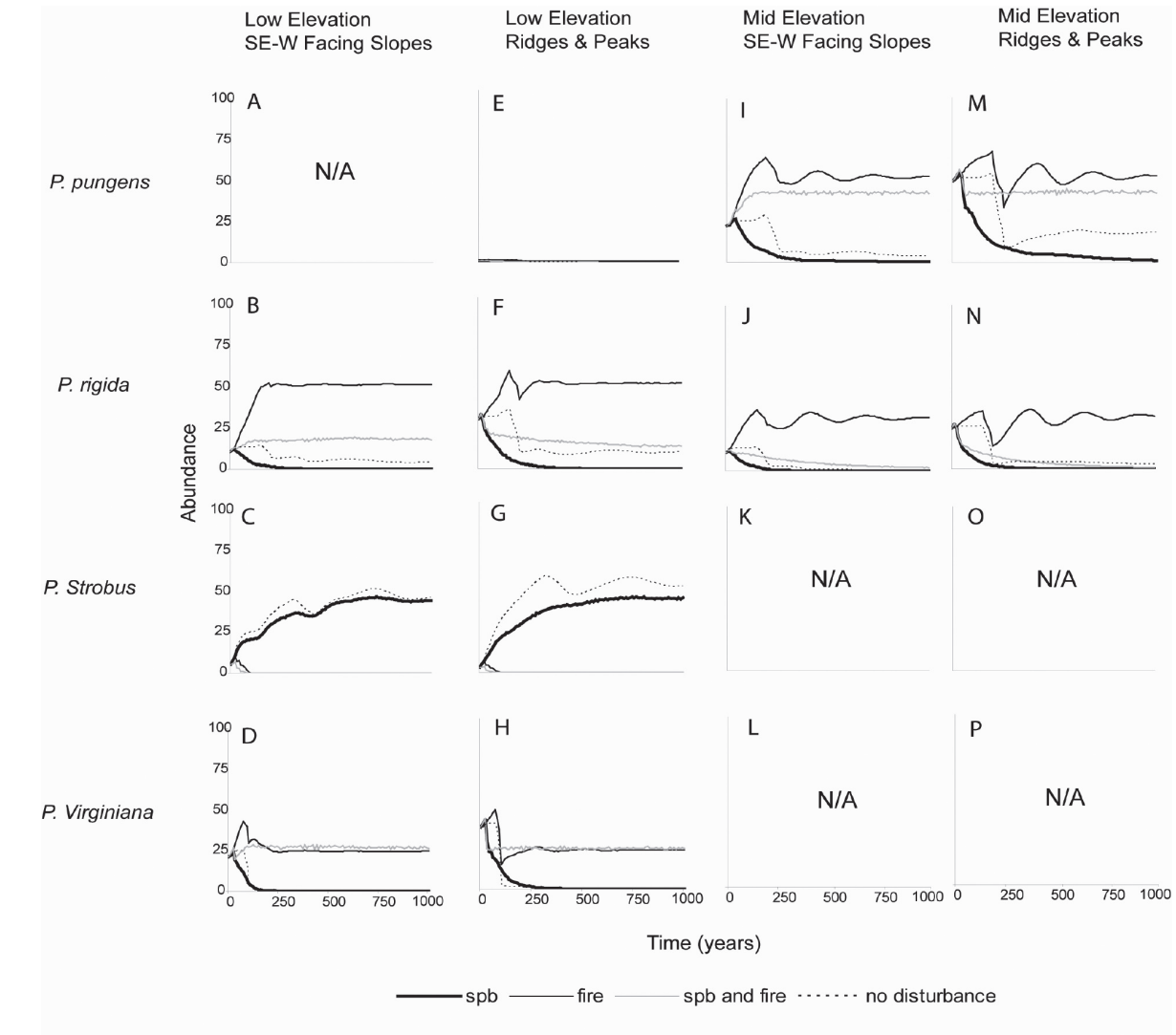

Fig. 2. Change in abundance (percentage of grid cells occupied) of Pine (all *Pinus* species) and Hardwood (non-conifer) functional types through time in each of four landscapes (Note: although *T. canadensis* was present in Mid-Elevation SE-W facing Slopes, the amount was negligible (<5% in all types) and therefore not represented in these graphs). Solid lines show average values for ten model runs, dashed lines delineate the maximum and minimum values returned for each of the ten model runs."

Discussion

The modeling projections presented here suggest that the regime of multiple interacting disturbances have important implications for the successional dynamics and vegetation characteristics in yellow pine woodlands of the southern Appalachian Mountains. When acting alone, fire was projected to create conditions favoring pine presence at levels higher than input, while SPB disturbance acting alone resulted in the removal of yellow pines. Additionally, our model projections suggest that a combination of fire and SPB disturbance creates sustainable yellow pine communities over the long term. This conclusion is consistent with the hypothesis that fire and SPB are part of a disturbance regime that maintains yellow pine woodlands (White 1987; Williams 1998; Harrod et al. 1998, 2000; Lafon & Kutac 2003). Our results also suggest that the combination of fire and SPB would maintain open woodland conditions more consistently and at a higher proportion than any other scenario. This vegetation configuration, which likely consisted of an understory of shrubs and/or grasses, is thought to have been typical of xeric sites in the southern Appalachians at the time of contact (Delcourt & Delcourt 1998; Harrod et al. 2000).

The only land type that did not fit the pattern of open conditions was mid-elevation SE-W facing slopes. In this land type, fire alone created more open conditions than did the combination of fire and SPB. This is directly attributable to the rise of one species, *Robinia pseudoacacia*. In the simulations, *Robinia* is present only on SE-W facing slopes. In the low-elevation simulations, *Robinia* became

Fig. 3. Change in abundance (percentage of grid cells occupied) of individual pine species with different disturbance scenarios.
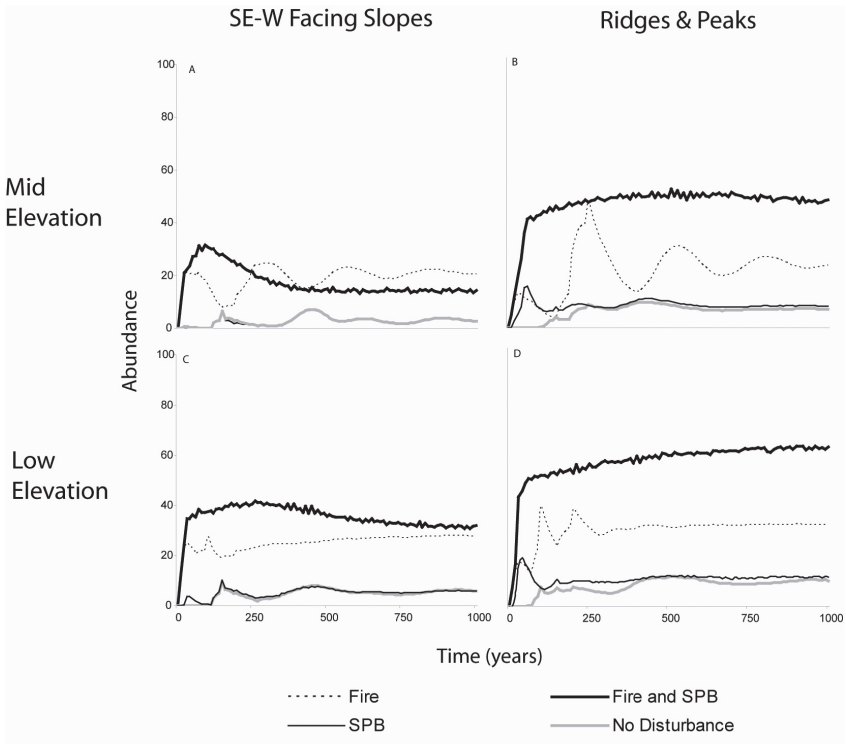
Fig. 4. Change in the abundance of open areas (percentage of empty grid cells) through time with different disturbance scenarios.
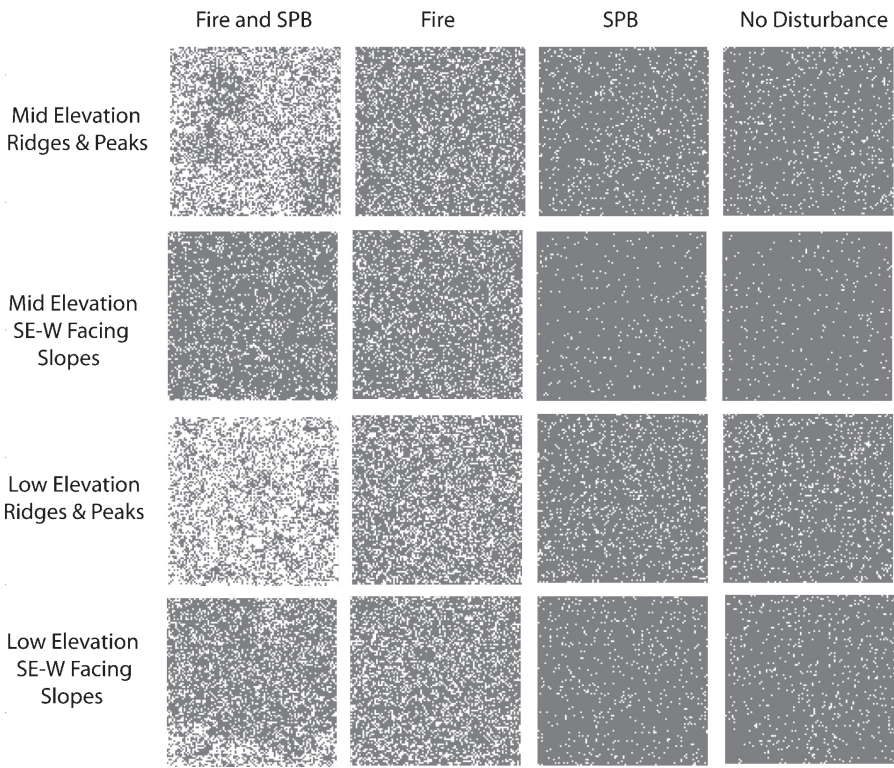
Fig. 5. Distribution of empty cells (white) versus occupied cells (gray) after 1000 years for all disturbance scenarios and land types.

dominant at year 750, and *Pinus virginiana* and *P. rigida* share dominance, but to a lesser extent. However, in the mid-elevation simulations, *Robinia* became dominant by year 350 and shared dominance only with *P. pungens*. The reason for this trend lies in the nature of *Robinia* as an extremely shade-intolerant and fire-intolerant species. While fire disturbance keeps *Robinia* populations low in the fire-only scenario, in the SPB/fire scenario gaps are created where *Robinia* can establish following the removal of pines by SPB. Once *Robinia* establishes under these conditions, it is very difficult to remove, because although it is intolerant of fire, it has a high probability of resprouting. Consequently, mid-elevation sites were converted to a *Robinia pseudoacacia /Pinus pungens* forest with relatively closed canopy conditions. These results are consistent with ecological data for the southern Appalachian region (Beck & McGhee 1974; McGhee & Hooper 1975). Boring & Swank (1984) found that *Robinia* dominated former *Quercus prinus* communities and became a major component in *Quercus coccinea-Pinus rigida* communities after clearcutting. However, they also noted that these stands eventually decrease in abundance as a result of locust stem borer (*Megacyllene robiniae*), which is a disturbance we did not simulate.

The results of this study yield several conclusions that are important to forest managers when undertaking restoration efforts. First, our projections suggest that *P. pungens*, more than any other species, thrives when in a disturbance regime combining SPB and fire disturbances on xeric sites. Because *P. pungens* is a southern Appalachian endemic, it is also important for biodiversity conservation (Zobel 1969). These factors suggest that *P. pungens* could be a species of particular interest for restoration efforts on low- to mid-elevation ridges and SE-W facing open slopes in the southern Appalachians. Second, the model projections imply that reintroducing fire would help maintain open pine stands similar to those thought to have occupied dry sites on Appalachian landscapes in the past. Such open stands would have low basal area and would not be conducive to the development or spread of large SPB infestations (Leuschner et al. 1976).

Several limitations should be considered in interpreting the results of this study. First, the LANDIS model design did not permit us to assess the contribution of SPB outbreaks to fuel loads and fire behavior. Second, we did not assess the impact of shrub, grass, and herbaceous species that may be important in the functioning of these systems. Third, our interpretations concerning open woodland conditions assume that the open cells would represent the conditions of grass and shrub presence. While open cells act as fire breaks within the model, they would act as fire conduits in a real-world setting. Future modeling efforts could incorporate these other functional types. Finally, because we used simplified landscapes to elucidate successional dynamics on individual land types, we do not address the influences of landscape structure on SPB infestations or vegetation dynamics. Hardwood forests occupying sites between the pine stands could impede the spread of SPB outbreaks on an actual landscape, but the effect of landscape structure on BDA-simulated SPB behavior has yet to be assessed. Regardless, SPB outbreaks often affect multiple pine stands in southern Appalachian landscapes because of the close proximity of the stands. The most recent outbreak, for example, disturbed pine forests throughout the entire region, producing severe declines in pine abundance. Our results apply to the restoration of such stands, and suggest that periodic burning will be required to maintain the compositional and structural integrity of stands affected by SPB. This conclusion is substantiated by empirical analogue (e.g. Harrod et al. 1998, 2000; Lafon & Kutac 2003) and by simulation modeling of fire effects on a landscape incorporating multiple land types (Lafon et al. In press).

The work presented here is part of a larger effort to apply LANDIS as a decision-making tool for restoration of southern Appalachian forests that are influenced by multiple disturbance agents. Our modeling results imply that while SPB can play an important role in maintaining these systems, the beetle could eventually lead to the destruction of xeric pine forests in the southern Appalachians if the key disturbance process of fire is not reintroduced. Because fire is an important part of the maintenance of these systems, it should be considered in developing management strategies. However, because the southern Appalachian Mountains exhibit complex and interacting climatic, topographic, and biological features, any restoration efforts would require careful consideration and planning.

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